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EDITOR

ALEXANDER WILLIAM EVANS

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JEAN BROADHURST
JAMES ARTHUR HARRIS
MARSHALL AVERY HOWE
MICHAEL LEVINE
GEORGE ELWOOD NICHOLS
ARLOW BURDETTE STOUT
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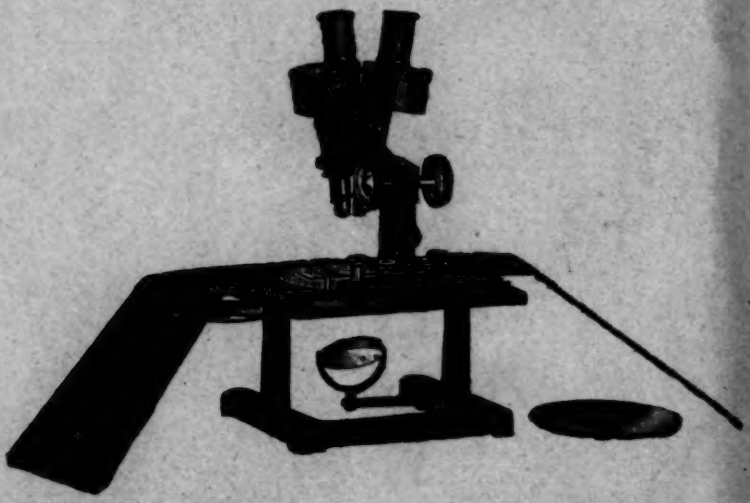

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Errata

Page 149, line 18, for "1–3" read "3–5."
Page 149, line 9 from bottom, for "1–3" read "3–5" and for "130" read "164."
Page 149, line 3 from bottom, for "130" read "164."
Page 150, line 6, for "130" read "164."
Page 287, line 15, for "Meriden" read "West Hartford."
Page 361, FIG. 4 should be numbered "5"; FIG. 5 should be numbered "6"; and FIG. 6 should be numbered "4."
Page 297, lines 16 and 17, omit commas; line 8 from bottom, omit first comma.
Page 310, line 7 from bottom, for "prairie coast" read "coast prairie."
Page 368, lines 24 and 29, for "mm." read "μ."
Page 446, line 4 from bottom, for "*parviflora*" read "*parvifolia*."
Page 452, line 16 from bottom, for "*latifolia*" read "*lateriflora*."

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BULLETIN

OF THE

TORREY BOTANICAL CLUB

JANUARY, 1920

Observations on monosporangial discs in the genus Liagora

MARSHALL A. HOWE

(WITH PLATE I AND FIVE TEXT-FIGURES)

The genus *Liagora* is a group of marine red algae of the family Nemalionaceae (Helminthocladiaceae). The species are confined to the warmer seas, where they show a preference for water that is normally agitated, ranging, however, from between the tide-lines on surf-beaten rocks down to a depth of at least one hundred feet. In the West Indian region, including Bermuda and southern Florida, the genus is represented by nine or ten species and one species is known to occur on the Californian coast. With the exception of one species, recently described from Bermuda by Collins & Hervey,* and one from the Mediterranean Sea, the plant body is more or less calcified, the amount of the lime and the way in which it is deposited being more or less characteristic of the various species. Under the compound microscope the thallus is seen to be of an obviously filamentous structure, both the structure and the often lubricous character of the plants when living sometimes calling to mind their fresh-water relatives of the genus *Batrachospermum*.

Most of the species of *Liagora* are consistently dioicous, others are consistently monoicous—characters that hitherto have been rarely ascertained or mentioned in the describing of species, probably because the antheridia are in some species very inconspicuous. The plants rarely seem to be sterile. Antheridia,

* Proc. Am. Acad. **53**: 100. 1917.

[The BULLETIN for December (**46**: 461–502. *pl. 19*) was issued December 31, 1919.]

procarps, or the subsequent cystocarps may nearly always be found, but the writer in examining some hundreds of specimens, has never seen anything that could be certainly interpreted as tetrasporangia or as a non-sexual alternating generation. In the older systematic works, it is either expressly stated that tetraspores in the genus *Liagora* are unknown or else silence is maintained on this point. In Schmitz's treatment of the genus in Engler & Prantl, Die natürlichen Pflanzenfamilien, we find, "Sporangien ungenügend bekannt, angeblich an knotig verdickten Stellen der oberen Thalluszweige aus den Endzellen der Rindfäden entwickelt und unregelmässig paarig geteilt." De-Toni, in his Sylloge Algarum, appears to have carried this statement over into Latin, omitting, however, to translate the "angeblich." Whether this statement by Schmitz rests upon his own personal observations or is based upon some previously published observation that has escaped the attention of the present writer is not clear. Oltmanns, in his Morphologie und Biologie der Algen, is apparently silent in regard to this matter.

In Kützing's Tabulae Phycologicae (**8**: 43. *pl. 90 I.* 1858) we find in his delineations of *Liagora Turneri* from the Red Sea a figure showing "Ein Gliederfaden, dessen eine Zelle sich zu einer Brutzelle erweitert, aus welcher sich die in *d. e. f. g. h. i.* dargestellten Knospen entwickeln, welche der Anfang der Seitensprossen sind." Structures evidently similar to those figured by Kützing occur in at least four of the West Indian species of *Liagora* (*L. ceranoides*, *L. valida*, *L. farinosa*, and *L. pinnata*), which often show small flat orbicular discs lying on the general surface of the plant or somewhat immersed among the assimilatory filaments. These discs are of a deeper red color than the main *Liagora* plant, they send down few or numerous roothairs from their ventral (proximal) surface in among the assimilatory filaments, and they bear on their dorsal (distal) surface a few sporangia, the contents of which remain undivided, so that they may referred to as monosporangia. Long, colorless, gelatinizing hairs may usually be seen, arising from this outer or dorsal surface. The disc is involved in mucus, the outer limits of which may be distinct or may be vague or imperceptible. Except in the youngest parts of the *Liagora*, this mucous envelope is more or less calcified. These

monosporangium-bearing discs look at first sight very much like independent epi-endophytes. Their darker red color, their dorso-ventral rather than radial symmetry, and the lack of any obvious genetic continuity with the *Liagora* give plausibility to the very natural first impression that they are independent organisms or perhaps obligate epiphytes of various species of the genus *Liagora*. Another plausible *a priori* hypothesis would be that they result from the germination of carpospores and represent a non-sexual alternating phase in the life-history of the *Liagora*. But in support of this latter hypothesis, the present writer finds no direct evidence at all, and the fact that in *L. farinosa* these monosporangial discs are commonly more abundant on antheridial than on cystocarpic plants would seem to point to its improbability. The truth seems to be that these discs arise from gonidia, gemmae, or aplanospores, derived from the terminal or subterminal cells of the assimilatory filaments of the *Liagora*, as was the view of Kützing in regard to similar structures in *Liagora Turneri*. Kützing appears to be the only one who has previously alluded to these structures in print and his observations appear to have been overlooked or ignored by subsequent writers on the genus. These monosporangial discs are especially common in West Indian specimens of *Liagora ceranoides* Lamour. (*L. pulverulenta* Ag.) and *L. farinosa* Lamour. (*L. elongata* Zan.), occurring on both antheridial and cystocarpic plants. In *L. ceranoides*, the gemmae are unicellular or bicellular, terminal or subterminal, solitary or concatenate, but are most frequently derived from the terminal (distal) cells of the assimilatory filaments. The cell enlarges, its contents become deeper red, its walls become soft and mucous, and a new cell wall is laid down inside the old one (FIGS. 1 and 2). Sometimes the rejuvenated cell or aplanospore escapes from the old wall before germinating, but nearly always in this species, as in *L. valida* Harv., germination takes place, or at least begins, *in situ*. The original wall, however, becomes so tenuous that the aplanospore or young disc is very easily detached from its place of origin and even when it develops in its original position, the original walls dissolve so completely that it is usually very difficult to assure one's self of its genetic connection with the filament from which it was derived. Occasionally, the cell, with its original

wall is abjointed as a one-celled gemma, but when abjointing occurs the subjacent cell commonly goes with it, the two together (FIGS. 7 and 8) constituting a two-celled gemma. In this case, the lower of the two cells seems not to divide but to persist as a finally inconspicuous stalk or appendage of the young disc, which results from divisions of the upper cell (FIG. 22). Very rarely (FIG. 28), one finds an irregular pluricellular gemma formed without obvious rejuvenescence or with rejuvenescence limited to one or two of its cells. Occasionally (FIG. 9) several consecutive

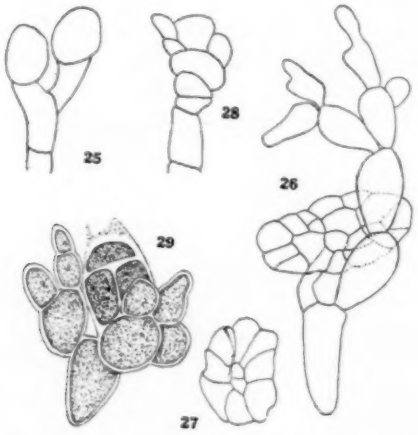

FIG. 25. Terminal cells of an assimilatory filament of *Liagora ceranoides* (No *4778d*, from Montego Bay, Jamaica), showing enlargement and rounding of two of them preparatory to their division to form multicellular gemmae, which develop into monosporangium-bearing discs. × 510.

FIG. 26. A later stage, showing young disc, still attached, disc and stalk-cell together corresponding to a twice forked vegetative branch four cells long (No. *4778d*), × 620.

FIG. 27. Dorsal view of a young disc, slightly smaller than that shown in FIG. 26 (No. *4778d*). × 260.

FIG. 28. Apex of an assimilarity filament showing irregular division to form a gemma (No. *3141*, *L. ceranoides*, Gun Cay, Bahama Islands). × 620.

FIG. 29. A gemma in a three-celled stage, the original mother-cell wall gelatinizing at apex (No. *3141*). × 510.

cells of a filament are converted into aplanospores with evident rejuvenescence and with gelatinization of the original walls. The first divisions of the rejuvenated cell appear to occur in a variety of ways. Often (FIGS. 8 and 29) they suggest the "cru-

ciate" or tripartite divisions of a tetrasporangium and structures of this character may have been responsible for the current somewhat vague and uncertain allusions to the existence of tetraspores in the genus *Liagora*. Occasionally the arrangement of the first segments of the young disc suggests that of the carpels of an orange, sometimes in apparent contravention of the usual rule that a cell divides in a plane perpendicular to its longest axis. When the young disc develops to a manifestly flattened form while still in its original orientation to the parent filament, it is seen (FIGS. 3, 4, and 6) that one of its edges is directed towards the filament, while the first root-hairs (FIGS. 5 and 22), ventral and central as regards the disc, are lateral in respect to the filament.

In *Liagora farinosa* Lamour. and *L. pinnata* Harv., the genetic connection of these discs with the *Liagora* is even more difficult to trace than in *L. ceranoides* and *L. valida*, owing, apparently, to the fact that the aplanospores are released from the more rigid mother-cell walls before germination, so that they do not germinate *in situ*. Hyaline, apparently unicellular hairs, usually several times as long as the diameter of the disc, arise from the dorsal surface and are probably always normally present in younger conditions at least, but owing to their delicacy and to their apparent readiness to dissolve into mucus, they are not always visible, especially in *L. ceranoides*, and they are not represented in our figures (FIGS. 6 and 18) of the disc in this species. The mature discs are suborbicular and are more or less similar in the four species of *Liagora* in which they have thus far been observed by the present writer, yet they show differences corresponding to the peculiarities of the species of which they constitute a part. In *L. ceranoides* and *L. valida*, the discs are softer, more mucous, and less compact than in *L. farinosa* and *L. pinnata*, in which the cells of the disc, like those of the assimilatory filaments of the main plant, have firmer, more rigid walls. In *L. valida*, the discs are thickened in the central part and often radiately unistratose towards the margins, while in *L. ceranoides* the discs give the impression of consisting of more than one layer of cells throughout. Fertile discs are mostly 90–230 μ broad (not including the mucous envelope), though in *L. farinosa*, the plants of which are commonly

the largest of the four species named, they may occasionally reach a diameter of nearly 400 μ. The monosporangia are ellipsoid, ovoid, or obovoid, and are usually 13–26 μ long and 13–18 μ broad, measuring protoplasts only. To what these monosporangia give rise on germination has not been determined but there seems to be some ground for believing that they produce monosporangial discs like those from which they sprang. Species of *Liagora* offer a favorable matrix for the germination of various filamentous algae, including species of *Acrochaetium*, *Ceramium*, and other Rhodophyceae, and inferences that young sporelings associated with a *Liagora* represent stages in development of the *Liagora* itself demand rigorous confirmation, such as might be supplied by cultures or by the presence of a complete series of developmental stages. In this connection, however, it may be remarked that the almost constant association of *Acrochaetium*-like forms with various species of *Liagora* is a suspicious circumstance that deserves further investigation.

In offering the above explanation of the origin of the peculiar monosporangium-bearing discs of certain species of *Liagora*, the writer realizes that he may be charged with having mistaken accidental contact for organic continuity. It would be easier, more conventional, and (*a priori*) more probable to regard the discs as independent or obligate epi-endophytes. Early in his acquaintance with them, the writer was at one time on the point of describing them as representing a new genus of uncertain family, but was deterred by observing that the character of the discs, particularly of their cells and cell walls varied according to the species on which they occurred, and that the discs were progressively older from base to apex of the *Liagora* thallus, the early stages being found only at the extreme apices. The chromatophores, too, seemed similar, except that those of the discs were more red than those of the vegetative cells of the *Liagora*, often as red as those of the carpospores. After much searching, indications that the discs could be traced back to certain cells of the *Liagora* thallus were observed, as shown in the accompanying figures. These observed evidences of direct continuity were not so numerous as the writer might wish and he knows of no analogy among other Rhodophyceae for the state of things here

alleged to occur in *Liagora*. However, he believes the above explanation of the origin of the discs to be correct and ventures to publish his observations in the hope that some one more favorably situated, perhaps with access to living material, with facilities for cultural experiments, and with a taste for cytological investigations, may be able to confirm or disprove them. The possibility that the discs represent an obligate epi-endophyte with a boring parasitic spore deserves special consideration.

THE NEW YORK BOTANICAL GARDEN

Explanation of plate 1

The material from which the drawings on this plate were made was obtained from four species of *Liagora*, all collected by the writer at Montego Bay, Jamaica.

1. Terminal cells of an assimilatory filament of *Liagora ceranoides* (No. *4778d*), showing enlargement and rounding of two cells preparatory to their division to form discs. × 620. (The relations of the branches have been somewhat disturbed and distorted by manipulation)

2. Enlarged terminal cell of an assimilatory filament of *L. ceranoides* (No. *5034*), showing gelatinization of apical portion of wall of original cell and formation of new wall for the rejuvenated cell. × 620.

3. A young few-celled disc of *L. valida* (No. *4778c*), still connected by mucus with the filament from the terminal cell of which it has apparently originated. × 375.

4. A young disc of similar size but with more numerous and smaller cells, the disc probably representing a branch of the filament against which it lies (No. *4778c*—*L. valida*). × 375.

5. A young disc showing its first root-hair and connected by mucus with the filament from the terminal cell of which it was apparently derived (No. *4778c*—*L. valida*). × 375.

6. A young disc in *L. ceranoides* (No. *5034*), with a mucus connection with the end of the filament from the terminal cell of which it was apparently derived. × 375.

7. A two-celled gemma in *L. ceranoides* (No. *4778d*) about to be abjointed. × 620

8. A later stage in the development of a similar gemma after detachment, the distal cell now divided into three cells and the proximal cell remaining undivided, forming a sort of stalk to the young disc (*L. ceranoides*, No. *4778d*). × 620.

9. The terminal portion of an assimilatory filament of *L. ceranoides* (No. *4778d*), showing the formation of several unicellular gemmae or aplanespores in a more or less concatenate series. × 510.

10. A supposed free aplanospore or unicellular gemma before its first division (*L. ceranoides*, No. *4778d*). Possibly, however, a spore from a monosporangium of a matured disc. × 510.

11. A young five-celled disc in which all of the divisions appear to have been lengthwise of the mother-cell, with the first root-hair originating from near one of the poles (No. *4778d*). × 510.

12. A young four-celled disc in which the first division appears to have been lengthwise of the mother cell, followed by the transverse division of one of the daughter-cells (No. *4778d*). × 510.

13. A later stage in the development of a disc, but showing a shorter root-hair (No. *4778d*). × 620.

14. An older stage, with long root-hair and with suggestion of a short stalk at one edge, indicating origin of the disc from a two-celled gemma as shown in Figures 7 and 8 (No. *4778d*). × 272.

15. Dorsal view of a young disc, suggesting discs of species of *Erythrotrichia* and *Erythrocladia* but apparently belonging in the present series (*L. valida*, No. *4778c*). × 510.

16. A later saucer-shaped stage, seen more or less edgewise, and showing three hairs springing from the dorsal surface in its thicker central part and one root-hair from its ventral surface (*L. valida*, No. *4778c*). × 272.

17. Dorsal view of a nearly mature disc with two monosporangia. The dorsal hairs have deliquesced or are so very inconspicuous that no attempt has been made to represent them. The dotted outer line indicates boundaries of the peripheral mucus or gelatinized outer walls. (*L. valida*, No. *4778c*). × 350.

18. An obliquely dorsal view of a mature disc with several monosporangia (*L. ceranoides*, No. *4778d*—edges of disc less monostromatic than in *L. valida*). × 272.

19. Escape of aplanospore from terminal cell of assimilatory filament of *L. farinosa* (No. *4775*). × 375.

20. A free aplanospore from the same plant (No. *4775*). × 375.

21. A young disc of *L. farinosa* (No. *4775*) in ventral view, showing first root-hair. × 620.

22. Another young disc in obliquely ventral view (No. *4775*), showing base of first hair from dorsal surface and first root-hair. × 620.

23. A mature or nearly mature disc of *L. farinosa* (No. *4775*), in lateral view, showing the more or less protuberant monosporangia. The dotted line indicates the boundary of the mucus envelope, which, in the natural state, is lightly permeated with lime. Only about one third of the length of the dorsal hairs is shown. × 272.

24. Obliquely dorsal view of a mature or nearly mature disc of *L. pinnata* (No. *4776*), with monosporangia, etc. × 272.

Studies in the conjugation of Spirogyra ternata

MABEL L. MERRIMAN

(WITH THREE TEXT FIGURES)

The discovery of but four chromosomes in *Spirogyra ternata* led to the collection of material in fruiting condition during the months of October and November, 1915 and 1916. The alga was growing under more or less unnatural conditions in a basin where the water was drawn off during the winter months. Its continued propagation seems uncertain as no trace of it was found in the fall of 1917 or 1918.

The large size of the nuclei, the low number of chromosomes, the few chromatophores, and the general transparency of the cells, combined with marked sexual differentiation of the filaments in conjugating periods, are features that make this species especially favorable material for the investigation of such debated questions as the potential bisexuality of vegetative cells, chromosome reduction, and the history of the secondary nuclei in the sporophyte generation. While material was at first studied with the hope of elucidation of these problems, continued study of the filaments brought to light interesting changes in the cells as they pass from the vegetative condition to a state of conjugation.

The diagnostic features of *S. ternata* Ripart (1876), as described by Collins (**2**, p. 114), are as follows: filaments 50–65 μ in diameter, with cells 1½–2 diameters long, somewhat swollen at the middle; zygospores ovoid, 45–66 μ in diameter, 1–1½ diameters long.

The form collected in 1915 varied from this in having its vegetative cells 74–80 μ in width. The zygospores in this 1915 material measured 64 μ in width and 120 μ in length. In the 1916 material there was much greater variability and frequent hybridization with a larger species resembling *S. jugalis* but differing in the shape of the fertile cell. The comparison of *S. ternata* with another species, *S. maxima*, growing under the same conditions and fruiting at the same season, revealed such great

differences in the form of the conjugating tubes and cell contents as to suggest the problems investigated in this paper.

A sinuosity is to be noted in the filaments in both vegetative and fruiting states, associated with a certain degree of motility. It is questionable which is the greater contributory factor to these movements, inequalities of growth or inequalities in the turgor of the cells, increased possibly by the mucilaginous layer on the cell wall. When in a state of conjugation the short portions of threads of *S. maxima* which are contained in the field of view under the low power of the compound microscope can be seen to be straight and to consist of large cells joined by small and narrow tubes. The fertile cells of this species are always unswollen. In *S. ternata* straight threads are rarely to be seen and then only in the earliest stages of conjugation, while a marked feature of the species is found in the swollen ♀ cells. The swelling often affects the cells throughout their entire length and sometimes increases their volume twofold, if the extensions of the conjugating tubes are taken into account. The filaments of *S. ternata* not only show a notable sinuosity, but in the curvatures of the filaments the two sexes always have a definite relation to each other, in spite of the fact that there are certain irregularities in the number of the cells. A comparison of numerous threads, whether lying in water or preserving fluids, showed that the filaments always assumed curves which varied from those slightly bent to those forming semicircles. Further examination disclosed the fact that the ♀ threads were invariably lying on the outer side of the curve, unless displaced or twisted in mounting. Often, in the water, the conjugating threads would naturally twist, but in so doing the ♀ thread, after a turn of a few cells, would again be found lying outside the ♂ filament.

S. ternata is an example of typical scalariform conjugation, for in the hundreds of filaments studied the movement in the conjugating cells was always found to be in one direction. It would be of interest to discover cases of cross conjugation, such as those reported by Cunningham (3) in a smaller species of *Spirogyra*. If forms of cross conjugation should be found, where regular alternating movements of contents take place, cells with straight outlines would seem probable, while if threads were found

containing several cells of one sex and then several cells of the opposite sex a zigzag position of the threads might be expected, instead of the symmetrical curves found in such a typically dioecious form as *S. ternata*.

It would seem that a continuous movement of contents of the ♂ cells in one direction, thereby increasing the contents of the ♀ thread as the zygospores form and subjecting it to a greater geotropic stimulus, would cause a sagging of the thread, resulting in its taking an outer or lower position in reference to the ♂ filament. Yet, in the majority of cases where the curvature was extreme and where the ♀ thread uniformly kept its position, there had been no appreciable movement of the contents, even when a complete formation of the conjugating tubes had taken place. This was evidenced by the fact that the chromatophores were unrelaxed in position and also by the intact connecting walls of the conjugating tubes. Since a large amount of conjugating material was available it seemed desirable to scrutinize more closely this relation of filaments in conjugation. It seemed possible that the degree of curvature might be dependent upon the amount of tumidity of the cells and not upon the degree of advancement in the formation of the zygospores. It was hoped also to bring to light more information as to the number and nature of the sexually potent cells and the manner of formation of the conjugating tubes.

Camera drawings were made of many pairs of filaments, in some cases numbering over fifty cells. A magnification of 140 diameters was used in order to have as many cells as possible in the field of view and yet to see clearly the position of the nuclei and chromatophores. Measurements of the drawings for length of the cells and filaments were obtained by two methods. In the first method a piece of thread held without undue tension, following the curving outer walls of the cells, was measured with the metric ruler. Slight discrepancies in this method would be due to the varying tension of the measuring thread. The other method employed, when it was desired to compare cell with cell instead of filaments as a whole, was to measure the distance from one transverse wall to the next with the ruler, not allowing for the convexity of the lateral walls. Such distances added would bring

out changes in the length of the filament as a whole but would not take into account differences in the two sides of the cell and in the extent of the cell walls.

For the ascertaining of these relations the two sides of the cell in each sex were measured in some of the most curved examples. The distance between the ends of the transverse walls opposite to the conjugating tube was taken in each case for measurement, as the various degrees of bulging of the inner walls where the tube emerged made accuracy difficult. When accurate measurements were needed to determine the size and position of the various cell organs, such as the nuclei and pyrenoids, higher powers and the ocular micrometer were used. Measurements of the drawings by means of the thread following the curving lateral walls always gave figures in excess of the sum of the lengths of the cells measured individually. Both of these methods, when so many hundreds of cells were examined, involved far less labor than the use of the ocular micrometer and gave the same relative proportions in the lengths of the cells.

The various measurements obtained in each series of observations have been arranged in tables. If a longitudinal series of cells is considered an individual plant, only a portion of a plant was measured in each case. It would, in fact, be impossible to be sure in collecting material that an entire thread, resulting from the germination of a zygospore, had been obtained. In this work, however, the cells of the *Spirogyra* have all been held as potentially the same.

Series A (FIG. 1) represents a pair of threads chosen for study by reason of their great convexity and torsion. In this series none of the opposing cells had apparently mingled their contents, and the nuclei are to be seen in their central positions with the chromatophores unrelaxed and contiguous to the cell wall, as in ordinary vegetative cells. In mounting these threads in the liquid on the slide the curvatures between *A* and *B* and between *C* and *D* in the figure projected much above the surface. Though a cover-glass was carefully lowered upon them the torsion was such that the flattening of the surface caused a breaking of the ♂ thread of the pair at *D*, one of the most curved points. Camera drawings were made of the threads as they were thus mounted,

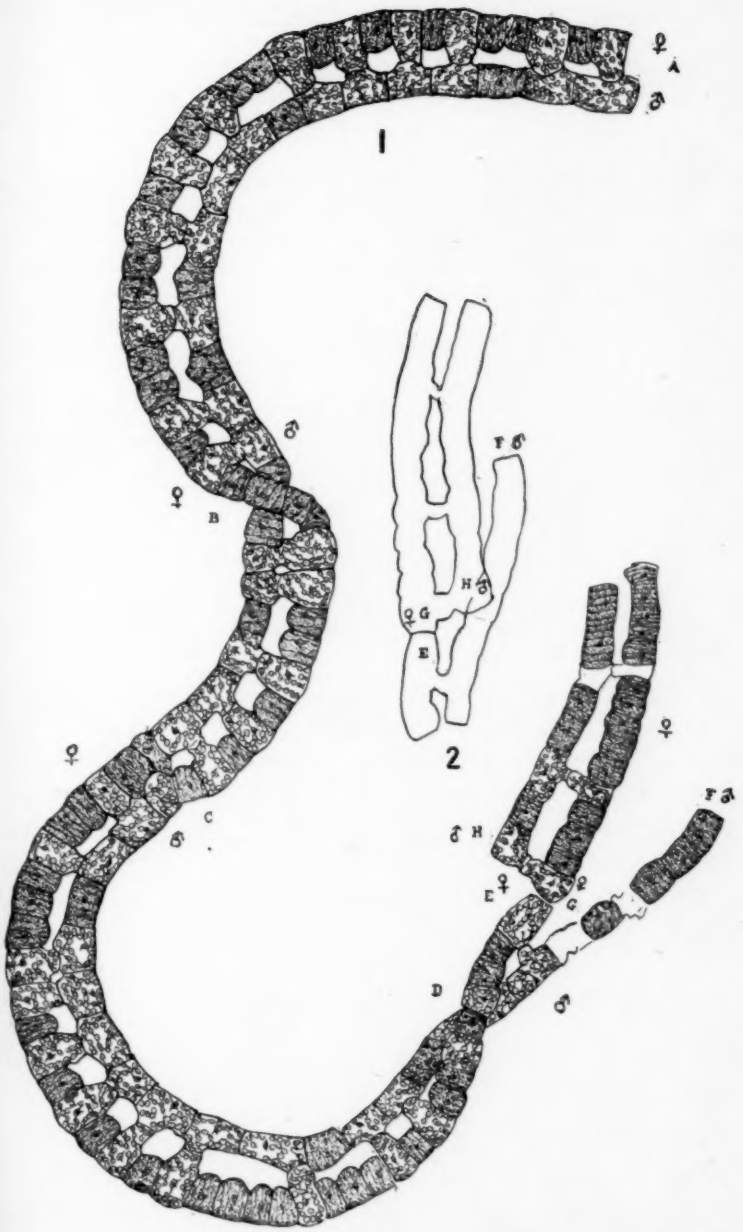

FIG. 1. A pair of conjugating filaments, showing torsion at points *B*, *C* and *D*; the ♂ thread is broken at *F*. × 140, reduced one half.

FIG. 2. A model of the broken filament replaced in its original position, showing relaxation in ♂ cells thatwere previously compressed.

the broken portion (upon lowering the coverglass) being reversed from its original position. FIG. 1 shows these threads as drawn originally, while FIG. 2, made by reversing a model of the broken threads, shows them as they were in their first position except for the break. The rupture of the thread reveals the previous tension of the cells. Upon severing the ♀ thread at *G* and then placing the terminal cell *H* of the ♂ thread next to the cell *F* from which it was broken, the ♀ thread, by reason of the relaxation of the ♂ cells in the breaking of the thread, lacks 45 mm. of meeting the cell *E* in the figure. When, on the contrary, the cell *G* is placed next to *E*, as in the model of the reversed cells, the thread shows a marked linear extension, indicated by the distance from *F* to *H*, the point to which *F* was previously joined. When this extension is measured by adding the distances between transverse

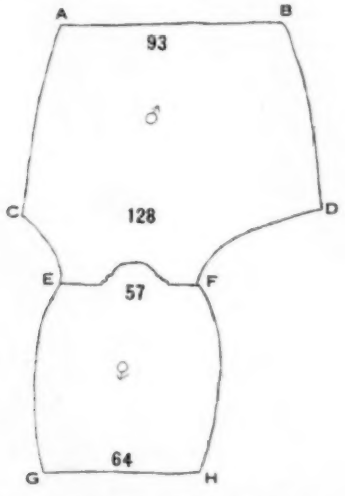

FIG. 3. Diagram of conjugating cells, illustrating distances between transverse walls as measured with the ocular micrometer.

walls it gives an excess of 43 mm.; when measured by a thread allowing for the curving walls, it gives an excess of 55 mm. These figures are an index of the amount of compression of the ♂ thread at this region of curvature.

The ♀ thread in this curved series, as shown in TABLE I, consists of ninety-five cells; thirty-six of these are conjugating

cells with their tubes formed, an equal number show by their tumidity an approach to the conjugating state, while only twenty-three show no signs of conjugation. Since there are only fifty-six cells all told in the ♂ thread it is obvious that many of the tumid ♀ cells would have proceeded to abortive conjugation. In the two portions of the filaments, *A–B* and *C–D*, where the curves are greatest and where in consequence the ♂ thread is under the greatest compression, it should be noted that the ♀ cells which show tumidity are opposite ♂ cells which have already conjugated. Seven conjugating cells in succession are included in the semicircular curve *C–D*, while in the curve *A–B* there is a succession of

TABLE I

SERIES A

Sex	Number of cells	Length of drawing of magnified filaments in mm. measured by thread	Sum of magnified lengths of cells, measured with ruler	Conjugating cells		Cells tumid, conjugating tubes not formed		Non-conjugating cells		Ratios	
				Number	Average length, microns	Number	Average length, microns	Number	Average length, microns	Potent cells (incl. tumid)	Non-potent
♀	95	779	701	36	63	36	48	23	42	.757	.242
♂	56	612	603	36	84	4	62	16	65	.714	.285
Excess.....	♀ 39	♀ 167	♀ 98		♂ 21	♀ 32	♂ 14	♀ 7	♂ 23	♀ .043	♂ .043

twelve conjugating or tumid cells with a single interruption. It is to be noted that the compression in the ♂ filament occurs before the rupture of the tubes and the mingling of the cell contents and hence before the relaxation of the chromatophores. In TABLE II the cells of Series A are grouped according to the length of the outer walls.

The next measurements taken were those of the distances between the outer and inner terminal points of the transverse

TABLE II

CELLS OF SERIES A ARRANGED ACCORDING TO LENGTH OF OUTER WALL

Length outer wall in microns	101–108	94–101	87–94	80–87	73–80	66–73	59–66	52–59	45–52	38–45	31–38	24–31	17–24
♀ conjugating.....			1		1	14	9	5	3	1	2		
♂ conjugating.....	2	6	4	5	14	2	2				1		
♀ tumid.....							2	10	10	7	6		1
♂ tumid.....					2	1				1			
♀ non-potent.....								3	7	7	3	2	1
♂ non-potent.....					4	3	3	3	2	1			

walls in each sexual cell. The significance of these measurements can be seen more clearly by taking as an illustration a single pair of cells, as in the accompanying FIG. 1. A ♂ cell, *ABCD*, has an outer wall, *AB*, measuring in a straight line 93 μ between the points *A* and *B*, this distance being less by 35 μ than a similar measurement in a straight line between the points *C* and *D* of the inner wall, from which the conjugating tube emerges. If the walls were originally an equal distance apart, as is the case in filaments where all the cells are non-conjugating and where external conditions are such as to cause no marked inequalities of growth in the two sides of the cells, *A* and *B* of the ♂ cell are brought nearer together, as conjugation proceeds, while *C* and *D* are spread farther apart. Internal pressure, the result of the metabolic activities of the protoplast, must cause this distension of *CD*. In the ♀ cell there is either no change whatever in the distance of *G* from *H* or only a slight increase. A study of the

TABLE III

CELLS A—B INCLUSIVE

LENGTHS GIVEN IN MICRONS

Number of ♀ cell	Length outer wall	Length inner wall	Outer wall increase	Conjugating with	Number of ♂ cell	Length outer wall	Length inner wall	Outer wall decrease
1	64	61	3	⟷	1	107	114	− 7
2	50	50	0					
3	71	71	0	⟷	2	100	96	+ 4
4	43	43	0		3	82	86	− 4
5	53	50	3					
6	64	64	0	⟷	4	79	89	−10
7	43	36	7					
8	57	50	7	⟷	5	79	79	0
9	61	57	4					
10	57	57	0	⟷	6	79	86	− 7
11	50	50	0					
12	71	64	7	⟷	7	71	86	−15
13	57	57	0		8	64	71	− 7
14	50	50	0					
15	64	64	0	⟷	9	71	86	−15
16	64	57	7					
17	79	57	22	⟷	10	107	129	−22
18	50	50	0					
19	79	71	8	⟷	11	100	107	− 7
20	64	64	0					
21	61	50	11		12	50	71	−21
22	79	71	8	⟷	13	86	100	−14
23	64	50	14		14	79	79	0
24	64	57	7		15	79	100	−21
25	71	71	0					
26	43	36	7					

membranes joining the completely formed conjugating tubes shows that the center of the tube pushes against the wall, forming a secondary smaller tube shown in the diagram. Probably it is the stretching of the wall as this tube presses against the wall of the cell that brings *E* and *F* nearer together.

Inspection of the TABLES III and IV, representing measurements of the cells where the curves in the filaments were greatest,

TABLE IV

CELLS C—D INCLUSIVE

LENGTHS GIVEN IN MICRONS

Number of ♀ cell	Length outer wall	Length inner wall	Outer wall increase	Conjugating with	Number of ♂ cell	Length outer wall	Length inner wall	Outer wall decrease
1	61	50	11	⟷	1	86	100	−14
2	43	36	7		2	79	100	−21
3	57	50	7					
4	64	50	14					
5	71	71	0	⟷	3	79	100	−21
6	57	57	0	⟷	4	79	86	− 7
7	43	43	0					
8	71	64	7	⟷	5	100	114	−14
9	50	50	0					
10	64	64	0	⟷	6	71	79	− 8
11	57	50	7					
12	64	57	7	⟷	7	93	107	−14
13	57	43	14					
14	71	64	7	⟷	8	100	107	− 7
15	50	43	7					
16	57	57	0					
17	42	42	0					
18	57	28	29					
19	57	50	7	⟷	9	111	128	−17
20	35	35	0		10	50	86	−36
21	50	50	0					

A—B and *C—D* inclusive, show the opposing numerical relations between the outer and inner walls of the two series.

From the comparison of the increases and decreases in the lengths of the walls in the two filaments a marked tendency is apparent toward lengthening the inner distance between the transverse walls of the ♂ cells, the corresponding distance between the transverse walls of the ♀ cells remaining the same or showing a slight decrease. The changes in length are brought about just before and during the process of conjugation. There is no reduction to be seen in any of the outer walls of the ♀ cells in these series, their excess lengths varying from zero up to 22 μ. In the case of the seventeenth cell, where there is the unusual in-

crease of 22 μ, the corresponding cell of the ♂ filament shows a reduction of 22 μ in the outer wall. This equality is presumably a coincidence, since the second ♂ cell in TABLE IV shows a similar reduction of 21 μ in the outer wall. This cell is not conjugating but is opposite tumid cells of the ♀ thread and is probably influenced by them.

In the ♂ filament there is a reduction in the outer wall in every cell but the second from the end *A*. In this cell it is to be seen that more of the wall than is usually the case takes part in the formation of the tube. All of this wall is elevated from the level of a straight line connecting the transverse walls. The bulging of this wall has probably counteracted the usual tendency of the inner parts of the transverse walls to spread apart.

According to these measurements, then, the compression in the filament, as revealed in the breaking and subsequent replacement of the broken parts, does not involve the filaments as a whole but is restricted in its extent to the parts of the cells which are farthest from the conjugating tube. Measurements also indicate that differences in tension in the ♀ cells are not so different from those occurring in vegetative cells. In this connection it is to be remembered that all the cells of a filament are in a state of slight compression, for when a filament is broken or an intervening cell dies the end cell extends slightly, rounding off and assuming the regular shape of an ordinary terminal cell. This does not explain the striking and opposing differences in tension found exclusively in cells in the conjugating state.

In another part of this investigation other changes in the conjugating cells will be considered, especially the formation of the tubes. There it will be noted that more of the inner wall of the ♀ cell takes part in the formation of the tube than is the case with the ♂ cell. Hence, as in FIG. 3, where *E* and *F* of the ♀ cell are always nearer relatively than *C* and *D* of the ♂ cell, the linear extension of the conjugating tube of the ♀ cell will be found to exceed that of the ♂ cell, if all of the linear extension pressing against the opposing wall is considered. However, it is the bringing together of the transverse walls and the consequent rectilinear contraction of one side of the filament at the beginning of conjugation that results in the constant relative positive of the

two sexes. This relative position was even maintained when *S. ternata* conjugated with the much larger species present. Whether a large ♀ cell of this species united with a small ♂ cell of *S. ternata* (the two differing by 32–50 μ in cell width), or whether a large ♂ cell conjugated with a smaller ♀ cell of *S. ternata*, this same relative position of sexes was maintained. The ♀ thread, whether larger or smaller, was always seen to occupy the outer position in the curve.

Studies will be presented also of the curvatures maintained in cases of triple and quadruple combinations of threads. Many examples were studied where one ♂ filament is conjugating with two ♀ filaments and, reciprocally, where one ♀ filament is conjugating with two ♂ filaments. Frequently a ♀ cell was found conjugating successfully with a ♂ cell on one side while the ♂ cell on the other side, though the conjugating tube had formed, showed only abortive conjugating. In the case of such an abortively conjugating cell it is important to note that the constant and marked inequalities in the distances of the transverse walls, seen in normally conjugating ♂ cells, were never exhibited. Except for its projecting tube the abortively conjugating ♂ cell, in the measurements between its transverse walls, accords more with those of the of the normally conjugating ♀ cell than with those of the normally conjugating ♂ cell. Abortive conjugation in *Spirogyra* has been previously reported by Bessey (**1**), Robertson (**5**) and, more recently, by Cunningham (**3**).

The work of Riddle (**4**) on the nature of sex in pigeons has a suggestive bearing upon these observations made on conjugating *Spirogyra*. He states, as a result of his extensive experiments, that sexual differentiation is to be interpreted as the expression of quantitative differences in the rate of protoplasmic activities, the more active metabolism resulting in males. With a low level of metabolism in the female is associated large size of yolk, low percentage of water in the yolk, high percentage of stored material, and a high total of stored energy. His review of the literature shows evidence of a relation between the rate of metabolism and sex in a great variety of animals, ranging from worms to man. Although his work and conclusions relate only to the animal kingdom he makes the conjecture that it would be of interest to

determine whether in dioecious plants there is a corresponding difference in the rate of metabolic exchange.

Since the ♂ gamete of *Spirogyra*, in contrast to the spermatozoön of animals, carries with it to the receiving gamete stored food as accretions about the pyrenoids, a high percentage of stored material does not occur in the ♀ cell until after conjugation is completed. The large proportion of swollen cells, both with and without conjugating tubes, and the fact that no visible movement of solid parts has as yet begun in the conjugating cells indicate that the different tensions shown by the measurements of the sex cells are to be causally connected with the differing amounts of tumidity and this in turn with different types of metabolism in the sex cells.

It would be premature to draw final conclusions from the intensive study of but one series. The comparison of Series A with other series observed, the tabulation of results and deductions as to potency of cells, formation of tubes and other related problems must be reserved for another paper.

HUNTER COLLEGE, NEW YORK CITY

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Some applications of the quadrat method

HENRY ALLAN GLEASON

By the quadrat method in ecological phytogeography is meant the intensive study of the vegetation or environment of a limited and definitely circumscribed area, known as a quadrat, in order to gain a comprehensive knowledge of the vegetation as a whole. The development of the method is the direct outgrowth of a need which has been felt by every ecologist who has seriously attempted the study of vegetational units. While its use is of great value and leads frequently to generalizations which would otherwise be difficult or impossible, it is not complete in itself, and ecologists are unable to rely upon it alone as a means toward successful field work. Indeed, its use to the exclusion of all other methods has never been suggested. It does constitute, however, the only practicable means for the quantitative study of the association, and as such it forms an important adjunct to photography and verbal description, which were previously the only feasible means of presenting the structure of vegetation. It also plays an important part in the study of associational dynamics, as migration and succession, and environometry.

It is exceedingly difficult and in many cases impossible for a reader to form a clear mental picture of an association from a written description, as may be demonstrated by a perusal of any discussion of an otherwise unfamiliar type of vegetation. The value of a verbal description is always greatly enhanced by photography. There are certain physical limitations to the value of a general photograph, caused by the difficulties of field photography and the necessity of reducing the print to the usual compass of a page, so that a general view of an association seldom gives a sufficiently clear idea of the vegetation, since the component species are distinguishable only in the immediate foreground, if at all. A detailed photograph of a small part of the association, on the other hand, is frequently made with difficulty and it is often impossible to choose for illustration an isolated portion which is

typical of the association as a whole. In the latter case, and in all cases of verbal description, the result unconsciously and unavoidably embodies the author's idea of the conditions, rather than the actual and impersonal facts, in that conspicuous species may be emphasized although possibly relatively unimportant, while important but comparatively inconspicuous species may be neglected. While the quadrat method is by no means a panacea for all these difficulties, its proper combination with verbal description and photography does much to aid the observer in securing a thorough knowledge of the association and in more satisfactorily expressing its structure in terms intelligible to his readers. The merit of the method lies not merely in the actual results which it affords but also in the deductions from and application of these results.

While quadrats may be of any chosen size, a single square meter is probably most frequently used. In the list quadrat, a simple list is prepared of the species included within it. In the count quadrat, the number of individuals of each species is also determined. Both of these are of value as a method, but are of little use in expressing results. For the latter purpose, the map quadrat is by far the most useful. A chart is prepared on a suitable scale, usually 1 to 10, and the location of each individual plant noted upon it. Other sorts of quadrats may be made for special purposes, concerning which reference may be made to the various works by Clements (1904, 1905).

The structure of a vegetational unit depends upon the species represented, determining the flora; on the relative number of individuals of each, determining by their form, size, and habit the appearance of the vegetation; and on the total number of individuals, determining the density of the vegetation.

The use of a chosen quadrat in representing this structure depends absolutely on the theory of the homogeneity of the association, which in turn depends on a number of factors (Gleason, 1917, p. 471). Given a uniform physical environment, the mere migration of some species over the whole area requires considerable time and interferes with the uniformity until it is accomplished, so that young associations are always less uniform than old ones, while in open associations migration may continue for a

very long period. Minor differences in environment may lead to the predominance of certain species in favorable places, to the persistence of relics, or to the early appearance of pioneers of other associations. Uniformity can not be perfect, although the general tendency of vegetation (apart from the effect of disturbing physical factors) is always toward uniformity, and it is most nearly attained in old (climax) closed associations, where entrance of new species is prevented by vegetative control of the environment, or in associations of extreme environment, where a small group of adjusted species enjoy a monopoly of the area.

If the association were absolutely homogeneous, if the plant individuals of the different component species were as regularly distributed as water and alcohol in a mixture of the two liquids, all quadrats of appreciable size would be similar and any quadrat could be chosen to represent the vegetation. Since no association is perfectly uniform, any one quadrat may by its structure accentuate the variability instead of concealing it. The value of a single quadrat also depends on its size and on the number of species in the association. In communities of numerous species (75 or more), a meter quadrat seldom includes as many as fifteen of them and usually contains still fewer. In very open associations, a meter quadrat frequently includes but a single individual plant. In either case, the error is reduced by increasing the size of the quadrat, but this simultaneously increases the labor of charting and decreases the value of a photograph.

The single quadrat of small size, one to two meters square, is therefore essential for graphic illustration, either by photograph or map, and is undoubtedly of value also for experimental work, but it fails to give a fair representation of the whole association, and is of less value as a basis for written description or as a unit for intensive study in field work. To be sure, a suitable quadrat may be chosen, but the quadrat method itself, as ordinarily used, offers no aid in the selection of this typical area, so the actual choice invariably represents the observer's idea rather than the impersonal facts.

The chief value of the quadrat method lies in the results obtained from the study of many quadrats, chosen at random to avoid the personal element, scattered over an area wide enough

to be representative of the whole association, of sufficient number to permit drawing logical conclusions, and of a size suitable to the character of the vegetation concerned. Several ecologists have devised statistical methods toward this end, which have been more or less successful. One of the earliest was Drude (1890), who described plants as social, gregarious, copious, or rare, depending on their number, their distribution, and their grouping. He also proposed the determination of the frequence of plants on a large scale by dividing an area into quadrats of 100 square kilometers. Pound and Clements (1898, 1900) adopted the same terminology in their first studies on the subject, but determined abundance within a single association by actual counts of the number of individuals in a quadrat 5 meters square, and investigated enough quadrats to warrant them in drawing averages. It is obvious, however, that averages from figures obtained in this way are not entirely trustworthy, since some species are mutually exclusive, while the averages might indicate that they normally grew together. Jaccard (1901) adopted the study of several adjacent quadrats as a method in his study of alpine vegetation, and developed the idea of the frequency index and the community coefficient. His results are, however, probably somewhat faulty, inasmuch as he used few quadrats in any one association and located them adjacent to one another. Harper (1917 and several other articles) has also attempted a statistical expression of carwindow observations, which corresponds to some extent to the frequency index as here used. Raunkiaer (1909) used essentially the same method described here.

The present writer first attempted the use of statistical methods to determine and express the structure of vegetation in 1903 (1907). He improved his method somewhat in 1908 (1910) and adapted it to class work with students in 1910. In the summer of 1911 he began the intensive study of the quadrat method and its applications at the Biological Station of the University of Michigan, and during the following four summers obtained a long series of data upon which the present paper is based. The statistics used in TABLES I and II were secured from the aspen (*Populus tremuloides* and *P. grandidentata*) association.

In practice, the following method is adopted. The size of the

quadrat to be used is determined first by the general character of the vegetation, using a small one, one square meter, for dense closed vegetation, and a larger one, two meters square, for open or irregular associations. The quadrats may be marked out by four stakes connected by a line of proper length, or they may be estimated by the eye with sufficient accuracy for all practical use. The optimum size can be ascertained after an examination of the preliminary results, and the survey can be repeated with a better size of quadrat if the first is unsatisfactory. The number to be counted depends upon the visible uniformity of the association, on the area covered by it and on the time available. If possible, one hundred are counted.

The first one is located anywhere. The others are located successively in a pre-decided relation to the first, thereby obviating any element of personal choice. Thus they may be in a straight line and separated by ten paces each, so that the whole strip of one hundred would be one kilometer long; or they may be in a square, but similarly separated, so that the area examined would be approximately 100 meters square; or any other arrangement of separate or contiguous quadrats may be used, depending upon the configuration of the association.

For the first quadrat, the species are listed and the figure 1 placed after each in a single vertical row. For the second, the figure 2 is placed after the 1 for all those species which occur also in the second quadrat, and new names followed by the figure 2 are added for the additional species. The process is continued to completion, when it is seen that some of the species occur in a majority of the quadrats and others in a few or only in one, and the common species are distinguished from the rare ones as the work proceeds.

At the conclusion of the count, the results are summarized and the ratio between the total number of quadrats and the number in which a particular species occurs is expressed as a percentage which is known as the *frequency index*, here abbreviated to *FI*. Thus, the frequency index of a common species may be as high as 100 and most associations show certain species with *FI* 90 or more, while others are as low as 1.

Obviously not every species of the association will appear in

the counts. Some of the rarer ones will be missed completely. For example, during five years experience in the aspen association of northern Michigan, during which some thousands of quadrats have been counted by the writer or his students, *Cypripedium acaule*, a plant of great rarity in this habitat, has appeared but once in the quadrats. These rarer ones, while of the greatest interest to the systematist or the phytogeographer in their relation to plant distribution in general, as emphasized so interestingly by Fernald (1919), and to the ecologist through the evidence which they frequently offer concerning the past or future development of the association, are nevertheless of negligible value in formulating a verbal description of the association. But the important species all do occur, provided the number and location of the quadrats has been properly chosen with reference to the size and character of the association, as the writer has demonstrated frequently in his own work.

If the whole association were included in a single quadrat, the frequency index of each species would be 100 and would give no idea of the comparative value of the species. In general, if the quadrats are too large, the frequency indices are also large and tend to approximate near 100. Conversely, if they are too small the indices are also small, and tend to approximate near unity, while the number of omitted species tends to become large and may even include some of the more important ones. The optimum size is one in which there is a wide divergence in the indices, from 1 to 90 or even more, so that the variation is an indication of the relative importance of the species. This is illustrated in the first three columns of figures in TABLE I,* of which the second column, based on quadrats two meters square, presents probably the best series of indices.

* The frequency indices given in TABLE I are not considered typical of the aspen associationi n general. The association consists of a sparse growth of two species of aspen and the paper birch, alternating with treeless areas dominated by bracken fern. The 240 quadrats counted for this paper were located entirely within a treeless area, and do not take account of the conspicuous difference encountered in the shade, where *Melampyrum lineare* and *Diervilla Lonicera* are both abundant. Neither do they cover an extent wide enough to give a fair representation of the treeless areas in general, since these omit completely such relatively common species as *Vaccinium canadense*, *Panicum depauperatum*, *Oryzopsis pungens*, and *Convolvulus spithamaeus*.

Again, the number of quadrats counted determines the accuracy of the frequency index as an expression of the ecological value of each species. The results from a small series certainly can not express the actual conditions as well as those from a large

TABLE I

	F/ in 15 quadrats of 16 square meters	*F*/ in 60 quadrats of 4 square meters	*F*/ in 240 quadrats of 1 square meter	*F*/ in every fourth quadrat	*F*/ in first 60 quadrats	*F*/ in second 60 quadrats	*F*/ in third 60 quadrats	*F*/ in fourth 60 quadrats
Pteris aquilina	100	100	99	100	98	100	97	100
Vaccinium pennsylvanicum	100	82	71	70	82	78	97	27
Gaylussacia baccata	80	67	48	43	60	25	87	22
Aster laevis	100	68	29	30	37	30	23	27
Carex umbellata	87	53	24	33	57	20	7	13
Rhus glabra	73	55	23	25	33	15	3	40
Rumex Acetosella	80	40	21	28	7	33	33	12
Rubus allegheniensis	40	30	17	18	37	15	10	7
Panicum boreale	60	35	16	17	5	12	17	32
Danthonia spicata	40	22	15	13	2	48	3	7
Gaultheria procumbens	47	27	14	10	7	20	25	5
Gnaphalium decurrens	60	33	12	15	2	20	17	8
Populus grandidentata	53	32	11	10	0	10	8	25
Hieracium venosum	60	28	8	7	3	7	5	18
Erigeron canadensis	33	20	7	8	5	0	2	22
Panicum xanthophysum	20	13	6	3	0	2	0	23
Diervilla Lonicera	13	8	4	3	15	0	0	0
Solidago canadensis	33	8	2	2	2	0	3	5
Agrostis hyemalis	27	8	2	3	7	2	0	0
Lactuca canadensis	20	7	2	2	3	0	2	2
Poa compressa	13	5	1	2	2	3	0	0
Epigaea repens	20	5	1	0	0	0	3	2
Quercus rubra	13	3	1	3	2	0	2	0
Comandra umbellata	7	2	1	2	0	3	0	0
Amelanchier canadensis	7	2	0	0	0	2	0	0
Hieracium paniculatum	7	2	0	2	0	0	2	0
Pinus resinosa	7	2	0	0	0	0	0	2

series. Repeated tests have shown that 100 is a satisfactory number and that no valuable increase in accuracy is gained by increasing the number beyond that, while it eliminates all computation in determining the frequency index.

Experience has also shown that better results are obtained if the quadrats are not contiguous, but separated by some distance, so as to cover more thoroughly the whole area of the association. In small associations, where even contiguous quadrats cover most of the area, this treatment is not necessary. If plants were

distributed absolutely at random over the association, that is, if the association were absolutely uniform throughout, separated quadrats would never be necessary. But plants are not distributed entirely at random. Each plant-parent gives rise to disseminules which occupy, roughly speaking, a circle about it, with a diameter depending upon the mobility of the disseminules. As early as 1903 the writer (1907, p. 159) was able to demonstrate these in his field work. As a check, the following data from 240 one-meter quadrats are offered. The 27 species have frequency indices ranging from 0 (1 quadrat only) to 99, based upon the whole series. If any fourth part of the series is taken as a basis, composed of 60 contiguous quadrats, as shown in the last four columns of TABLE I, the average discrepancy between the two series of indices is 6.8, or for the 15 commonest species 10.7, and the difference may be as high as 44 for a species which normally grows in patches. But if every fourth quadrat is taken as a basis, that is, 60 separated quadrats, as shown in column 4 of TABLE I, the greatest discrepancy is only 9 and the average only 1.9, or 2.7 for the commonest species. In other words, 60 quadrats well scattered give results practically as reliable as 240 contiguous ones.

From a list of the frequency indices, made from quadrats of suitable size and number, the species are arranged in order of their general distribution in the association, and any number of them may be segregated for further study as the most typical or commonest. Since the frequency index increases with the size of the quadrat, a quadrat of proper size may now be chosen which will normally include all the more important species as well as a number of the less important ones also. The size of this *major quadrat* may be determined in advance and, in field work with students, one of them assigned to each student for detailed study and description. Although every such major quadrat may not actually contain all the important species, the student may be assured that it is nevertheless a fair sample of the association as a whole. The value of setting a definite area before each student, in which he may do his more intensive work, will be at once apparent to every teacher who has tried to present this phase of ecology in the field. The method of determining the major quadrat will be discussed below.

The relative abundance of a species is a fair measure of its ability to maintain itself under the conditions of environment and competition prevalent within the association. Long-established species of an old association have frequently become diffused thoroughly over the whole area, and their abundance may be determined by counting, but recent immigrants into old associations or any species of young associations are not uniformly distributed. The number of individuals of such plants is therefore zero in those parts which they have not yet reached and is too high to show their relative adjustment in those parts which they have reached.

But there is a definite relation between the number of individuals of a species and its frequency index. If only one is present in the area covered by the quadrats, the frequency index naturally cannot exceed 1. If only two are present, it can not exceed 2 and may be only 1 if both happen to occur in the same quadrat. While it is possible for a species to be represented by a large number of individuals all of which occur in a single quadrat only, the chance of such a thing actually happening is very small indeed. Similarly, while 100 individuals might be so thoroughly distributed that they would occur one in each quadrat, there is again very slight probability of it. The mathematical possibilities are capable of solution according to the laws of probability and chance. If n plants are scattered at random over q quadrats, the probability of any one quadrat being occupied is expressed by the formula $1 - \left(1 - \frac{1}{q}\right)^n$. Thus for 2 plants in 5 quadrats $1 - \left(1 - \frac{1}{5}\right)^2 = 0.36 = FI\ 36$. Or for 65 plants in 100 quadrats $1 - \left(1 - \frac{1}{100}\right)^{6/5} = FI\ 48$. Or, conversely, FI 48 should indicate a total of 65 individuals within the 100 quadrats. But since plants are not distributed entirely at random, the actual number is therefore always greater than indicated by the mathematical formula, which may be expressed, when $q = 100$, as $n = \frac{\log (1 - FI)}{\log 0.99}$. Thus, *Pteris aquilina*, determined by actual count to have an average abundance of 4,400 in 100 quadrats, has FI 99, corresponding to a theoretical number of only 455 individuals. Obviously, the

discrepancy between actual and theoretical number should be, and is, greatest in species of high frequency, *FI* 95 or more. It is not possible to draw any accurate conclusions as to the relation between theoretical and actual number of individuals, but in general, the theoretical number is one fifth to two thirds as large as the actual, and results any more accurate than this are probably of little or no value in ecological description.

The determination of the proper size of the major quadrat involves reducing the original series of quadrats to a smaller number of larger quadrats, thereby increasing the frequency index of selected species to 99 or more. With *FI* 99 or more for all the important species, it may be assumed that this quadrat is large enough to serve as a fair sample of the association.

In the original equation $1 - \left(1 - \frac{1}{q}\right)^n = FI$, substitute for q the number of quadrats actually counted, use for *FI* the index of the least common one of the important species, and solve for n. Substitute again the determined value for n and 99 for the original *FI* and solve for q. The equation is $1 - \frac{1}{q} = \sqrt[n]{.01}$ (presuming 100 quadrats were counted), from which q may be easily determined. For example, in a certain association, it is desired to determine a major quadrat which will probably contain all the species with *FI* 60 or more.

$$1 - \left(1 - \frac{1}{100}\right)^n = 60\text{: } n = 90$$

$$1 - \frac{1}{q} = \sqrt[90]{.01}\text{: } q = 20 \text{ (fractions omitted)}$$

That is, the original 100 quadrats redivided into 20 larger quadrats should show *FI* 99 or 100 for all species which originally had *FI* 60 or more; or the major quadrat should be five times as large as the original. The error concerned in computing the value of n, due to imperfect distribution of the species, does not affect this last equation, and experience has shown that it gives surprisingly good results. On the average, four major quadrats out of five, the location of which is chosen at random, present all the important species for which they were computed.

Jaccard's *community coefficient* (*CC*) was designed to express by a number the degree of similarity between two areas of vegetation. His method is to divide the total number of species in both areas into the number common to both. Thus, two areas, each containing 30 species, of which 20 were common to the two, contain a total of 40 species, and the community coefficient is accordingly 50. Jaccard's method fails to take account of the much greater importance of some abundant species, and the resulting error of computation may be obviated, in part at least, by weighting each species with its frequency index. Referring to columns 5 and 6 of TABLE I, and weighting each species with its average index in both columns, the results, shown in TABLE II

TABLE II

	In first area only	Common to both areas	In second area only
Pteris aquilina		99	
Vaccinium pennsylvanicum		80	
Gaylussacia baccata		42.5	
Aster laevis		33.5	
Carex umbellata		38.5	
Rhus glabra		24	
Rumex Acetosella		20	
Rubus allegheniensis		26	
Panicum boreale		8.5	
Danthonia spicata		25	
Gaultheria procumbens		13.5	
Gnaphalium decurrens		11	
Populus grandidentata			5
Hieracium venosum		5	
Erigeron canadensis	2.5		
Panicum xanthophysum			1
Diervilla Lonicera	7.5		
Solidago canadensis	1		
Agrostis hyemalis		4.5	
Lactuca canadensis	1.5		
Poa compressa		2.5	
Quercus rubra	1		
Comandra umbellata			1.5
Amelanchier canadensis			1
	13.5	433.5	8.5

are obtained, from which the community coefficient of the two areas concerned is determined as 95, by dividing the sum of the three columns, 455.5, into the sum of the center column.

By Jaccard's method, giving equal weight to each species, 24 total species divided into 15 common species = *CC* 62.

This method, while doubtless better than the original one, is still deficient in allowing equal weight to such small slender plants as *Erigeron canadensis* and large bushy ones as *Gaylussacia baccata*. If each plant could be further weighted by a multiplier expressive of its size, a better index would doubtless be attained. In this particular case, for example, each plant of the latter species occupies probably 400 times as much ground space as the former. So far no serious attempt has been made to follow out this suggestion.

It is freely admitted that the expression "*FI* 55" means little to a person who has not already experienced its meaning by actual field work. But to such persons it does present at once an idea of the relative abundance of that particular species, and an idea much more accurate than any such general expression as *common*, *rare*, or *copious*. Students who have used the method adopt it into their scientific vocabulary and actually use it in their conversation, almost as freely as they refer to degrees of temperature. The writer has heard a student, describing the luxuriant growth of *Epilobium angustifolium* following a recent fire, state that it must have had "a frequency index at least 90," instead of resorting to the usual hyperbole to express great abundance, or, in alluding to a new station for a *Habenaria*, say "There was a good deal of it all through the woods: *FI* probably 5 or 10." And if such a student should read an account of an utterly unfamiliar vegetation in some remote part of the world, in which the frequency indices were given, he would at once have a relatively clear idea of the actual conditions.

Nevertheless, the quantitative study and description of vegetation are still in their infancy, and there is every opportunity for great improvement.

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1914–1919

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Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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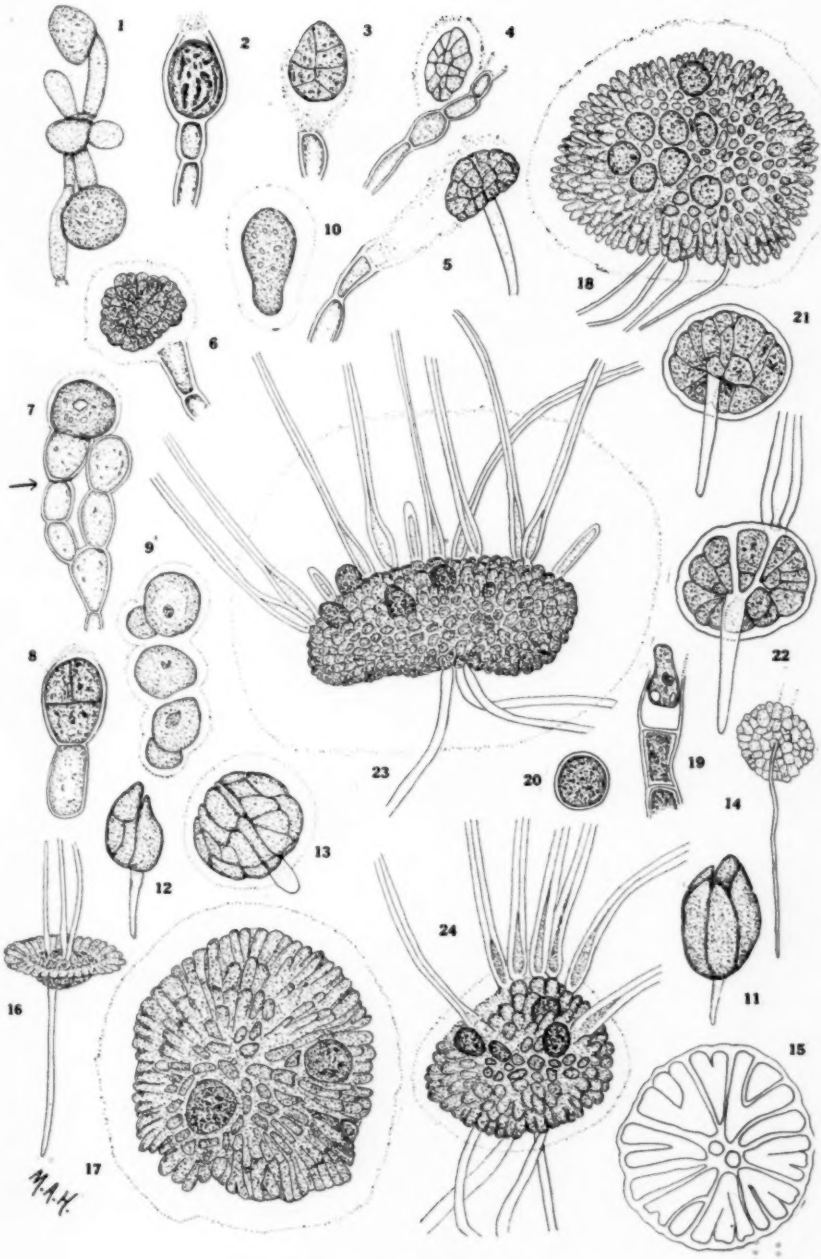

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